Effects of Increased Loading on *In Vivo* Tendon Properties: A Systematic Review

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ABSTRACT

WIESINGER, H.-P., A. KÖSTERS, E. MÜLLER, and O. R. SEYNNES. Effects of Increased Loading on *In Vivo* Tendon Properties: A Systematic Review. *Med. Sci. Sports Exerc.*, Vol. 47, No. 9, pp. 1885–1895, 2015. **Introduction**: *In vivo* measurements have been used in the past two decades to investigate the effects of increased loading on tendon properties, yet the current understanding of tendon macroscopic changes to training is rather fragmented, limited to reports of tendon stiffening, supported by changes in material properties and/or tendon hypertrophy. The main aim of this review was to analyze the existing literature to gain further insights into tendon adaptations by extracting patterns of dose-response and time-course. **Methods**: PubMed/Medline, SPORTDiscus, and Google Scholar databases were searched for studies examining the effect of training on material, mechanical, and morphological properties via longitudinal or cross-sectional designs. **Results**: Thirty-five of 6440 peer-reviewed articles met the inclusion criteria. The key findings were i) the confirmation of a nearly systematic adaptation of tendon tissue to training, ii) the important variability in the observed changes in tendon properties between and within studies, and iii) the absence of a consistent incremental pattern regarding the dose-response or the time-course relation of tendon adaptation within the first months of training. However, long-term (years) training was associated with a larger tendon cross-sectional area, without any evidence of differences in material properties. Our analysis also highlighted several gaps in the existing literature, which may be addressed in future research. **Conclusions**: In line with some cross-species observations about tendon design, tendon cross-sectional area allegedly constitutes the ultimate adjusting parameter to increased loading. We propose here a theoretical model placing tendon hypertrophy and adjustments in material properties as parts of the same adaptive continuum. **Key Words:** PATELLAR TENDON, ACHILLES TENDON, PLASTICITY, DOSE-RESPONSE RELATION, TIME-COURSE RELATION

Hitherto regarded as mere connections between muscle and bone, tendons have become the object of increasing scrutiny in the past four decades. Research has since highlighted the duality of tendon function, trade-off between an effective limb actuation and their viscoelastic behavior (8,50) enabling muscle power attenuation and amplification, energy conservation (34,47,64), and protection against muscular damage (18,50). Hence, tendon adaptation to changes in mechanical constraints seems essential to maintain movement efficiency and reduce the risk of damage.

Notwithstanding the low occurrence of fibroblasts and rather limited vascularity, tendinous tissue displays anabolic, mechanical, and morphological changes when exposed to increased loading. After acute exercise or training, collagen synthesis is elevated (48,49,57,58), with scarce evidence of collagen degradation (48). Accordingly, microdialysis analyses suggest an increase in extracellular matrix (ECM) enzymes involved in collagen turnover, such as matrix metalloproteinases (31,35). Furthermore, an upregulation of stress-responsive cytokines and growth factors (e.g., insulin-like growth factor or transforming growth factor-ß-1) has been observed in the Achilles tendon (AT) *in vivo* (22,60), the patellar tendon (PT) *in vitro* (68), and in animal tendons (23–25) after repeated muscle contractions. The common belief is that newly synthesized molecules are deposited into the fibrillar structure to repair and/or optimize it for daily loading configurations. In line with this hypothesis, research indicates that short- and long-term exposures to increased stress lead to tendon material and morphological changes (e.g., 2,21 for review). In many cases, increased loading causes an elevation in stiffness—or resistance to deformation—and the Young's modulus, which characterize material properties as a measure of stiffness when tendon dimensions are taken into account (1,45,66). Other studies also showed decreases in hysteresis (13,43,63) and increase in tendon cross-sectional area (CSA) (9,19,66). From a structural point of view, an increase in stiffness could be linked to either changes in material properties or a larger CSA. However, because of discrepant results of intervention studies, the relative contribution of

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material and morphological changes to the alterations in tendon mechanical properties with increased loading remains largely elusive. Furthermore, some authors have reported contrasting findings regarding the nature and the magnitude of adaptations to training (e.g., 33,55). Existing reviews based on selected research articles (21,53) have provided critical analyses of tendon adaptive responses to training. Here, we propose to obtain better understanding of this topic via a systematic approach and a meta-analysis with the aim of gaining some insights into the patterns of tendon adaptation.

The main purpose of this meta-analysis was to extract existing data to investigate i) the dose–response relation between increased tendon loading and adaptations and ii) the time-course of material and morphological changes. Eventually, this analysis also aimed to propose a theoretical model for the relative contribution of these changes to the mechanical plasticity of the PT and AT.

METHODS

Search strategy and inclusion criteria. The computerized bibliographic electronic databases PubMed/MEDLINE, SPORTDiscus, and Google Scholar were initially searched from July to the end of December 2013 by H. P. W. The combination of the following key words were used: PT or AT and plasticity, adaptation, strength, endurance, ultrasound, MRI, stiffness, the Young's modulus, stress, hysteresis, loading, exercise, cross-sectional area, and mechanical properties. In addition, references cited by all eligible articles were systematically considered. The term "stretching" was not searched because this activity imposes only a small fraction of the tendon loading experienced during resistive exercises or running.

Eligibility criteria. Peer-reviewed studies were eligible if they were in English language and analyzed healthy human tendons *in vivo*. Review articles, conference abstracts, or commentaries were not taken into account. Articles should include either pre- or posttraining data or tendon characteristics in subjects with different backgrounds of long-term physical activity or with different side-to-side loading history. Such criteria were exclusively fulfilled by studies on the PT and AT, with the first one published in 2001 (44). To avoid the influence of maturation-related tendon growth, studies had to be conducted among healthy and uninjured sample groups with a mean age above 19 yr. Measurements of changes or differences in at least one of the material and mechanical (Young's modulus, stiffness, hysteresis) or morphological (CSA) properties had to be provided in the publication or predictable via calculations (see "Data extraction and analyses" section). To ensure that tendon mechanical properties were obtained from the linear portion of the load–deformation curve, studies were included only if tendon testing had been performed at a level above 50% of the individual or common maximal force/torque. Studies combining resistance training with other forms of exercise were excluded because they did not allow isolation of a particular training effect. Studies reporting the acute effects of exercise were also excluded because these allegedly reflect properties such as fatigue resistance, which are distinct from the adaptive processes reviewed here. All articles were checked against these inclusion criteria by one author (H. P. W.).

Methodological quality assessment and risk of bias. The methodological quality of the included studies was analyzed with a quality appraisal tool adapted from Galna et al. (16). This scale used in systematic reviews consists in the rating of proposed qualitative criteria. Criteria relate to both internal and external validity, reflecting the accuracy of the measurement and the generalizability of the results. Each question on the quality appraisal tool was rated "1" when the criterion was met, "0" when it was not met or information was missing, and "0.5" if the criterion was partially met. Hence, a higher total score indicated a higher quality of research. Criteria were checked and agreed upon for each article by two investigators (H. P. W. and A. K.).

Furthermore, the risk of bias was assessed by considering three relevant criteria for this review, as follows: random assignment, inclusion of a control group, and blind testing and/or analysis.

To assess the strength of the influence of training upon tendon mechanical properties, mean and SD of stiffness differences after training (intervention studies) or between subjects (comparison studies) were used to calculate the standardized effect. The 95% confidence intervals were calculated using the standardized effects, the degrees of freedom, and the corresponding *P* values (sportsci.org/2006/wghcontrial.htm). When the exact *P* value was not provided in the text (1,3,4,7,10,33,44,55,63,65), a "worst case" *P* value of 0.05 or 0.01 (as appropriate) was used. Tendinous stiffness was chosen because it was nearly systematically reported in studies on tendon adaptations and because the probability for this variable to be altered by training is supposedly higher than the Young's modulus or CSA.

Data extraction and analysis. Data were extracted by H. P. W. and O. R. S. When numerical values were missing, they were estimated from digitized figures if available (ImageJ version 1.48v, National Institutes of Health, Bethesda, MD). Because percent changes in relevant variables were not readily accessible in all reports, relative changes were calculated by dividing postintervention mean values by baseline mean values. Training studies with a longitudinal design had a duration shorter than 6 months (with one exception (19), which had a duration of 9 months) and were considered as short-term loading. The effects of long-term loading was assessed via the reported differences between tendons of individuals with a long (i.e., years) training history and controls or via the side-to-side differences in tendon properties of athletes after years of sport-induced asymmetrical loading. For the quantification of the dose–response relation between increased loading and measured tendon properties, the effects of strength training were considered in relation with i) contraction modes, ii) exercise frequency, intensity, and volume, iii) and subjects' training status. The terminology of muscle action was adapted from Wernbom et al. (72) and included dynamic external resistance (DER) (concentric or eccentric) and isometric resistance (IR). The training volume was calculated in arbitrary units (sets × repetition × intensity). Unfortunately, a proper quantification of training volume via tendon stress or strain was not possible because the majority of studies do not report this information. Therefore, training intensity was associated with the load used during training, quantified as a function of the one-repetition maximum (e.g., 80% of one-repetition maximum). Training frequency was quantified as the number of sessions per week. Because plyometric and endurance training do not allow estimation of actual tendon loading, these types of interventions were excluded from the analysis of the dose–response relation. However, the effects of plyometric, endurance, and sprint training were included in the rest of the analysis as distinct categories from DER and IR. Generally, all studies lacking a sufficient description of training methods or the training load to allow the calculation of training volume were also excluded from the dose–response analysis. Classification of training status in untrained, moderately trained, trained, advanced, and elite volunteers (10) was not possible because of a lack of available details. In most of the studies, the subjects were described as either untrained or physically active. However, none of the physically active participants had engaged in any systematic strength training for at least half a year. For this reason, the training status of all subjects at baseline of training studies was deemed comparable with that of the untrained control subjects of cross-sectional comparisons, enabling a broader time frame of analysis. The influence of training duration upon the analysis of dose–response relations was accounted for by dividing percent changes in tendon Young's modulus, stiffness, and CSA by the number of training days. Because of the too limited amount of data (five studies), changes in hysteresis could not be included in the dose–response and time-course analyses.

RESULTS

Search results and study characteristics. Of the 6440 articles found in databases, the literature selection process yielded 35 original articles (see Figure, Supplemental Digital Content 1, Flow chart of search strategy and selection process, http://links.lww.com/MSS/A479). Most of the retained studies exclusively included male participants (*n* = 26) or mixed sexes (*n* = 7), whereas only a couple of articles focused on female participants (*n* = 2). The study sample size ranged from seven to 35 participants, with a mean sample size of 10 ± 3 and 12 ± 7, respectively, for all selected PT and AT studies. The mean characteristics of the participants (age, 28 ± 13 yr; height, 175 ± 6 cm; mass, 72 ± 7 kg) were comparable in studies on the PT (age, 32 ± 18 yr; height, 174 ± 6 cm; mass, 72 ± 7 kg) and the AT (age, 25 ± 4 yr; height, 177 ± 5 cm; mass, 71 ± 7 kg). Training interventions lasted between 6 and 14 wk or between 8 and 14 wk, respectively, for the PT and AT. The sample groups were trained using DER (PT, *n* = 10; AT, *n* = 11) and IR (PT, *n* = 2; AT, *n* = 4) muscle contraction modes, plyometric (AT, *n* = 4) and endurance training (PT, *n* = 1; AT, *n* = 1). DER training commonly consisted of a combination of concentric and eccentric muscle actions to lift and lower the weight (PT, *n* = 13; AT, *n* = 9). Only four studies looked at the influence of a specific contraction mode (PT, *n* = 1; AT, *n* = 3).

The influence of long-term increased loading was explored in 10 (three PT and seven AT) cross-sectional studies. These studies looked at the effects of long-term endurance running (PT, *n* = 1; AT, *n* = 6), sprinting (AT, *n* = 2), resistance training (PT, *n* = 1), and volleyball (AT, *n* = 1). The influence of asymmetrical side-to-side loading history was also evaluated in one study (PT) on fencers and badminton players.

Effects of training on tendon properties. The initial agreement (Cohen's kappa) between reviewers for the methodological quality assessment scores was satisfying (PT, κ = 0.81; AT, κ = 0.79; SPSS Statistics version 22.0.0; SPSS Inc., Chicago, IL). Overall, the quality assessment yielded a moderate score (see Tables, Supplemental Digital Contents 2 and 3, Summary of quality appraisal for individual studies (PT), http://links.lww.com/MSS/A480, and Summary of quality appraisal for individual studies (AT), http://links.lww.com/MSS/A481, respectively). Of 10 points, PT studies scored 5.16 ± 2.06 points and AT studies scored 5.03 ± 1.68 points (ranging 5–7 points for both tendons). However, scores were largely limited by two criteria, the consideration of covariates and internal validity, which were almost never disclosed. In addition, authors often failed to report sufficient details to enable the readers to repeat the protocol. This point particularly held true for the data processing and the nondisclosure or incomplete disclosure of techniques and algorithms used in the analysis of ultrasound scans.

Figure 1 displays the changes in muscle strength and tendon properties after a period of increased mechanical loading. Because studies could include more than one training group, the number of data points exceeds the number of studies. The data did not enable considering the influence of sex, age, or physical status because of an insufficient number of studies addressing these factors. In addition, we did not observe any appreciable difference between the effects of dynamic or isometric muscle actions on tendon adaptation. Hence, all analyses were performed irrespective of these factors.

Three main observations can be made from this figure, as follows: i) changes in tendon energy storage/release capacity (hysteresis) have received far less attention than changes in stiffness, ii) tendon material, mechanical, and morphological properties can undergo substantial modifications when exposed to external short- and long-term increased mechanical stimuli (e.g., Young's modulus and stiffness > 80%, hysteresis greater than −30% and CSA > 30%), iii) the magnitude of these changes greatly varies between studies, with percent changes ranging from −16.4% to 84.2% for the Young

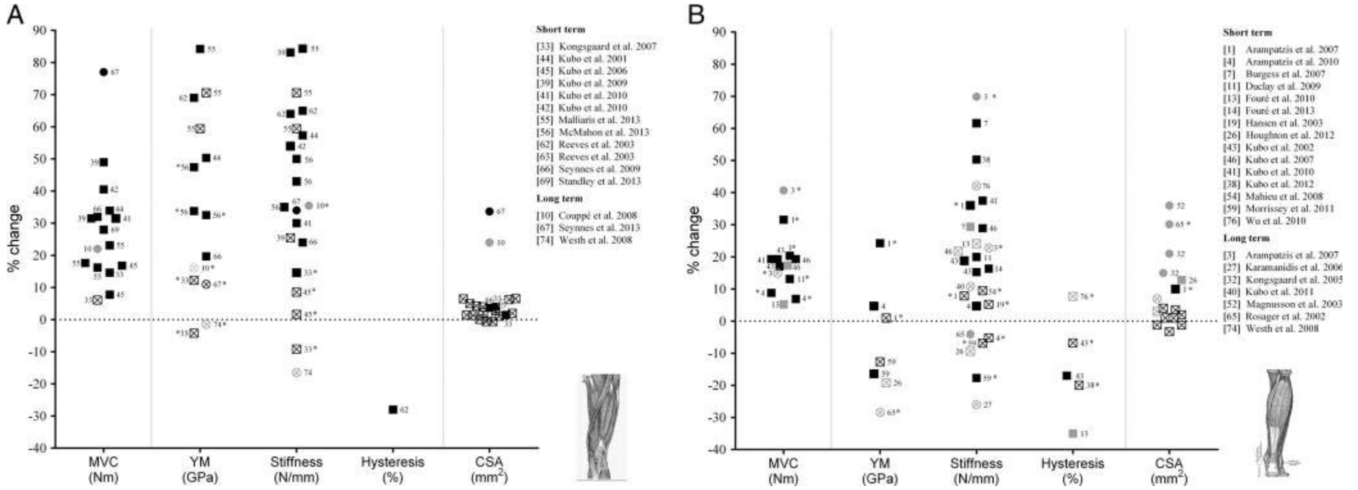

FIGURE 1—Effects of physical training on the properties of the PT (A) and AT (B) measured *in vivo*. Changes in material, mechanical, and morphological tendon properties in response to short-term training interventions (*squares*) and long-term comparison studies (*circles*). Changes in maximal voluntary contraction torque of the knee extensor and plantarflexor muscles are shown in the "MVC" column. *Filled symbols* indicate significant changes, and *hollow crossed* symbols indicate nonsignificant changes. Extracted values (see "Data extraction and analysis" section) are distinguished from readily available values with an *asterisk*. *Black symbols* refer to data obtained with a training type favoring high load transmission, without a need for storage and release of elastic energy in the tendon (i.e., resistive exercise). *Gray symbols* refer to data obtained with a training type requiring storage and release of elastic energy in the tendon (i.e., running and plyometrics). For clarity, references to nonsignificant changes in the PT (39,41,42,44,45,55,56,62,74) and AT (1,4,13,19,38,41,43,74) CSA were not included in the figure.

modulus, from −26.0% to 84.3% for stiffness, or from 1.4% to 36.0% for the tendon CSA. In addition, within-group SD for change scores (6.0%–81.8%) indicate highly variable individual responses. Nevertheless, with the notable exception of endurance training, all the training types considered in this review seemingly have the potential to elicit an increase in tendon stiffness. Long-term running training was never associated with higher tendon Young's modulus or stiffness.

As shown in Figure 2, the training effect upon tendon mechanical properties is strong. Most of the experiments included at least one control group, but the use of inactive control subjects was often replaced by references to separate reliability measurements. Instead, many studies were designed to compare two groups with different training interventions. Nearly all studies were conducted without blinding, which constitutes a noteworthy risk of investigator bias.

Dose response. Figure 3 shows the relations between training parameters and changes in PT and AT properties. Seventeen (eight PT and nine AT) studies were included in the analysis of the dose–response relation of tendon adaptations to training.

The mean training volume was 1076 ± 567 (arbitrary units, $n = 13$) and 1290 ± 962 (arbitrary units, $n = 9$), respectively, for the PT and AT. The mean training intensity seemed similar between the knee extensor and plantarflexor tendon (PT: 77% of MVC, $n = 8$; AT: 82% of MVC, $n = 9$). Likewise, the mean training frequency was 3.2 ± 0.6 times per week for the PT ($n = 12$) and 3.5 ± 1.2 times per week ($n = 8$) for the AT.

In the PT, the daily increase in the Young's modulus, stiffness, and CSA was 0.64% ± 0.22% ($n = 5$), 0.68% ± 0.29% ($n = 9$), and 0.04% ± 0.02% ($n = 3$) on average, respectively. In the AT, these values reached 0.15% ± 0.14% ($n = 2$), 0.45% ± 0.41% ($n = 9$), and 0.10% ($n = 1$) for the Young's modulus, stiffness, and CSA, respectively. From the scatter plots of Figure 3, neither training volume nor intensity or frequency emerged as apparent covariates of changes in tendon properties.

Time course. Figure 4 demonstrates that resistance training elicited a nearly systematic stiffening of tendons (27% ± 26%) to a similar extent after 6–8 wk than that after 12–14 wk. The magnitude of training-induced changes in stiffness was also comparable with the differences (34%) observed between long-term resistance-trained athletes and controls (67). The increase in the Young's modulus paralleled (22% ± 35%) the changes in stiffness within the first weeks of training. However, we did not find any report of increased Young's modulus in individuals with a history of long-term loading. On the other hand, tendon CSA was consistently larger (approximately 34%) in long-term athletes than that in controls whereas tendon hypertrophy was limited (3% ± 4%) and rarely reported with short-term training. In all cases, larger CSA were only observed in certain tendon regions.

DISCUSSION

The present meta-analysis confirmed a nearly systematic change in tendon properties with training. A sizable increase in tendon stiffness occurred in nearly all intervention studies, seemingly at a higher rate for the PT than that for the AT for a given training volume. The appraisal of training-induced changes in tendon properties revealed an important variability between and within studies. Furthermore, no consistent incremental pattern was observed regarding the dose–response or the time-course relation of tendon adaptation within the first months of training. Instead, these relations suggest that a rapid increase in the Young's modulus is often paired with tendon stiffening and that this parameter remains elevated in a rather monotonic fashion within the first months of training. However, long-term (i.e., years) training was associated with a larger tendon CSA, without any evidence of differences in material properties.

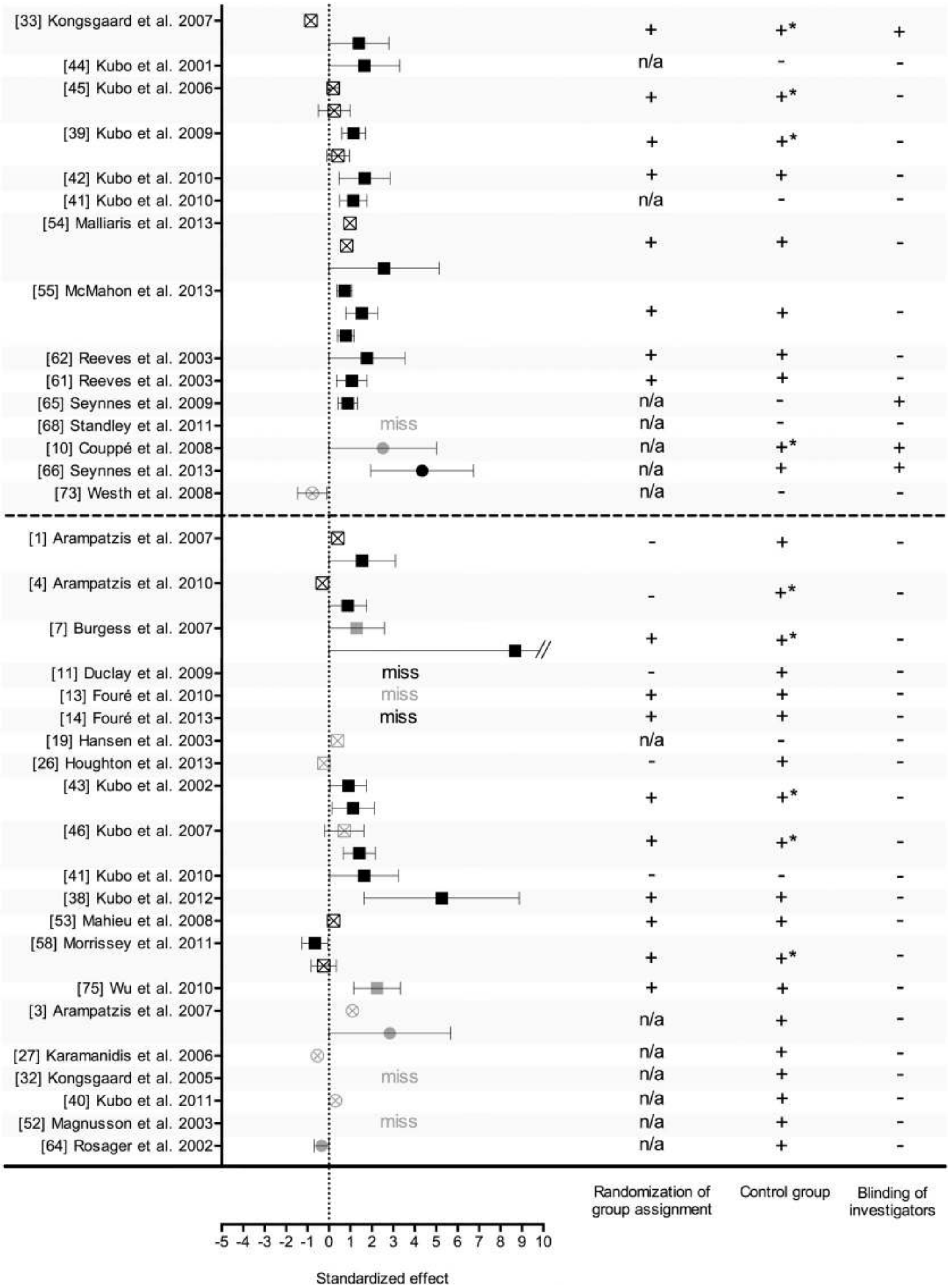

FIGURE 2—Standardized effect and risk of bias. Standardized effect and confidence intervals for changes in tendon stiffness in response to short-term training interventions (*squares*) and for differences in tendon stiffness between long-term athletes and controls (comparison studies, *circles*). Studies focusing on the PT and the AT are grouped above and below the *horizontal dotted line*, respectively. *Filled symbols* indicate significant changes, and *hollow crossed* symbols indicate nonsignificant changes. *Black symbols* refer to data obtained with a training type favoring high load transmission, without a need for storage and release of elastic energy in the tendon (i.e., resistive exercise). *Gray symbols* refer to data obtained with a training type requiring storage and release of elastic energy in the tendon (i.e., running and plyometrics). Miss, relevant data unavailable; n/a, not applicable (single group design and comparison studies); + Indicates met criteria; - indicates unmet criteria; * indicates only one active control group.

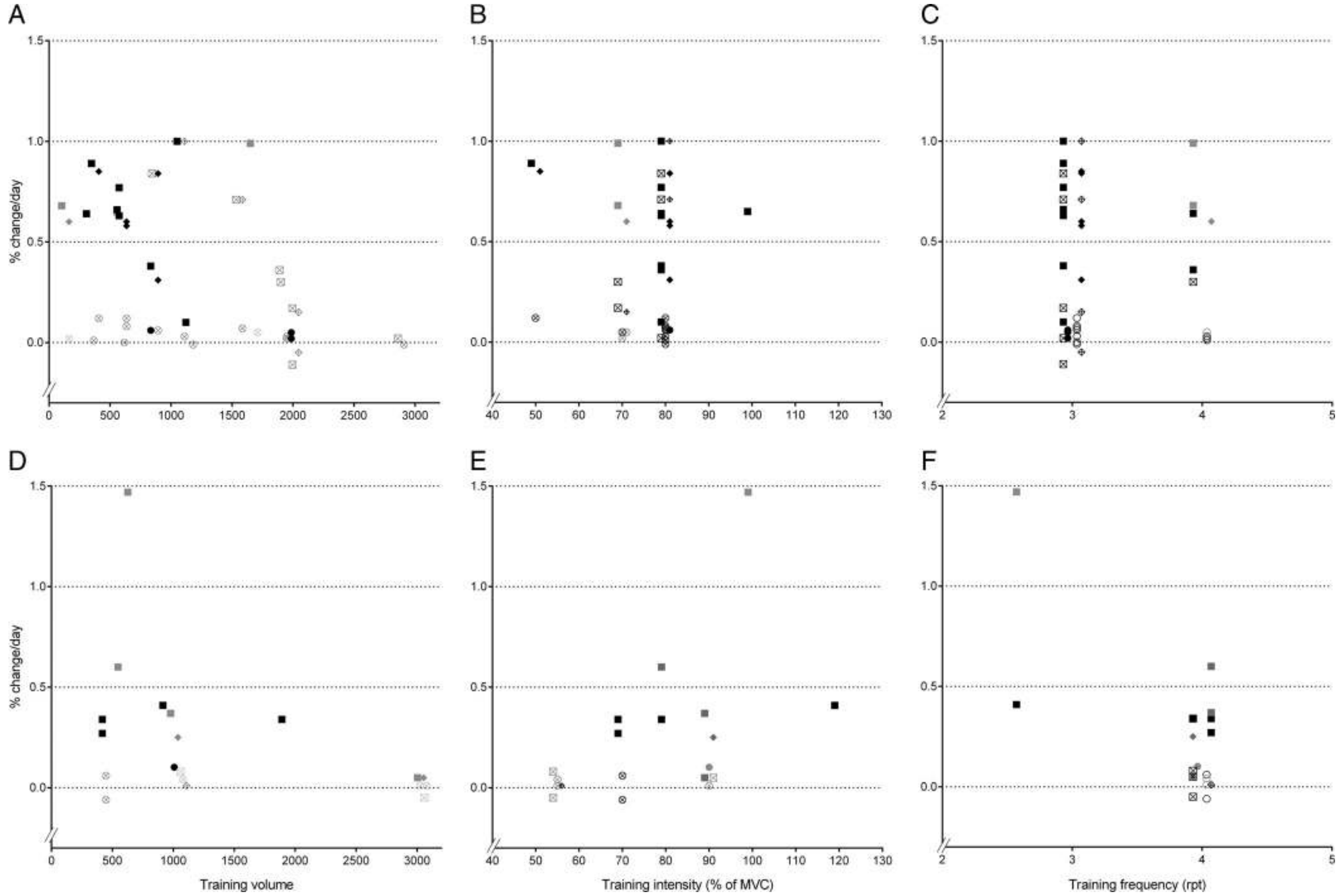

FIGURE 3—Dose–response relation of the effects of resistance training on the PT (A, B, and C) and AT (D, E, and F). Percent daily increases in tendon Young's modulus (*rhombus*), stiffness (*square*), and CSA (*circle*) against training volume, intensity, and frequency, respectively, are shown. *Black filled symbols* denote data obtained after training involving muscle dynamic contractions, and *gray filled symbols* denote data obtained after training involving muscle isometric contractions. *Hollow crossed symbols* refer to nonsignificant changes.

Adaptations in the PT and AT. In addition to the confirmation of rapid adjustments in tendon properties to an increase in maximal loading, the present meta-analysis yielded a number of observations, which could not be made from single studies taken separately. Some of these observations contradicted common assumptions about tendon adaptation. For instance, differences in the adaptive responses of the PT and AT could be expected between these tendons because of their distinct anatomy (5,70), function (47), and metabolic activity (37). However, our analysis does not support this assertion and both tendons displayed comparable adaptations in terms of material, mechanical, and morphological properties after training (Fig. 1). Changes in the AT modulus may seem lower than those in the PT at first glance, but this impression is caused by a single data point from the only study (59) that found significant decrease in tendon stiffness and modulus after resistance training. Furthermore, Figure 1 shows that the number of reports on training-induced changes in modulus is relatively lower for the AT (five of 22) than that for the PT (nine of 15).

Beyond the consistency of tendon adaptations, this analysis also unveiled the important variability in the magnitude of training-induced changes. The phenomenon allegedly results from the variety of testing and analyzing methods. Some important factors are briefly mentioned in the present review, but the reader is referred to relevant literature for more detailed information on these aspects (e.g., 12,17,21). The influence of one of these methodological factors is illustrated in Figure 1; changes in stiffness and the Young's modulus seem higher on average in studies using resistive exercise than in those using a training type with "spring loading" configuration (e.g., plyometric training and endurance running). This observation is in agreement with the theory of a functional influence upon tendon adaptations (see "Adaptive mechanisms and model" section). It suggests that resistive exercise is better suited to reinforce the effective "load transmission" role of tendons than other forms of exercise requiring energy storage and release.

Data variability is often bound to measurement reliability. The agreement of repeated measurements was difficult to evaluate in the present review because of the few training studies reporting the consistency with which main outcome variables were obtained. The few available data indicate a satisfactory reproducibility, with coefficient of variations of 4.7%–11.7% for measurements of AT stiffness (13,19,43,76).

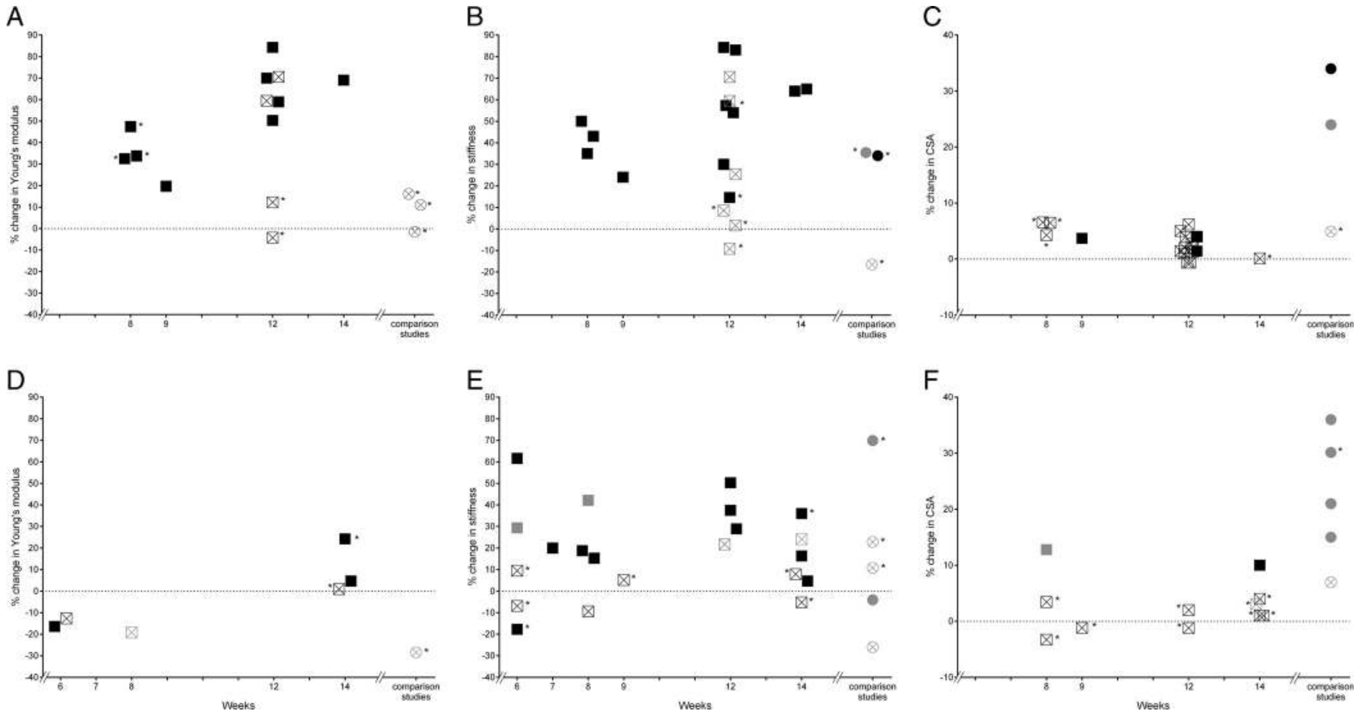

FIGURE 4—Time-course of average changes in the Young's modulus, stiffness, and CSA of the PT (A, B, and C) and AT (D, E, and F). Differences in tendon material, mechanical, and morphological properties after short-term training interventions (*squares*) and between long-term athletes and controls (comparison studies, *circles*) are shown. *Filled symbols* indicate significant changes, and *hollow crossed symbols* indicate nonsignificant changes. Extracted values (see "Data extraction and analysis" section) are distinguished from readily available values with an *asterisk*. *Black symbols* refer to data obtained with a training type favoring high load transmission, without a need for storage and release of elastic energy in the tendon (i.e., resistive exercise). *Gray symbols* refer to data obtained with a training type requiring storage and release of elastic energy in the tendon (i.e., running and plyometrics). Confidence intervals were included as *error bars* when sufficient information was available for their calculation (i.e., mean and SD of changes).

For tendon CSA, coefficients of variations around 1.5%–7.5% for the AT and 0.6%–0.7% for the PT were reported (results obtained with ultrasonography or magnetic resonance imaging). Yet, Figure 1 shows that training-induced changes in these variables are sometimes very close to 10%, which may have limited the ability of some authors to detect smaller changes and prevented a precise appraisal of the time-course and dose–response relations.

Dose response. Despite the obvious influence of increased daily stress and strain, none of the considered training parameters seemed related to tendon adaptations in a dose–response manner. As shown in Figure 3A–F, no incremental pattern could be observed between training volume, intensity or frequency, and daily changes in tendon properties. However, for a given training volume, the daily stiffening rates seemed to be higher in the PT (approximately 0.8% per day) than those in the AT (approximately 0.4% per day). The slower response of the plantarflexor tendon seemed to be confirmed when looking at the influence of training intensity and frequency (Fig. 3B–C and E–F) and may be attributable to distinct physiological responses of PT and AT to acute exercise (e.g., 37).

The effect of training volume or frequency does not seem to have been investigated in intervention studies, but the present findings are at odds with a few training studies (1,4,33) demonstrating the influence of training intensity on tendon adaptations. This disagreement may partly be attributable to the relatively small number of available studies and to the fact that tendon loading intensity and volume should ideally be quantified using stress and strain parameters rather than force (1,4). In addition, certain methodological issues or disparities (see 21) may have hindered between-study comparisons. For example, nearly all studies retained for this review used discrete loading durations during tendon testing regardless of strength increments due to training. It follows that, for a given contraction duration, posttraining increases in strength resulted in higher loading rates and, possibly, affected the measurements of tendon stiffness (36). Another example is linked to the lack of available information regarding the contraction durations used in various training protocols. The index of training volume used in the present analysis could not include this parameter, which reflects the time during which tendons are under tension. However, this aspect is certainly driving the amount of microdamage caused to the tendinous structure (71,72) and should ideally be taken into account when looking at adaptive responses. Collectively, these findings indicate that future interventions should i) use stress and strain to quantify training load, ii) use common testing standards, and iii) last for less or more than 12 wk to provide a more reliable reading of the dose–response relation between tendon adaptations and training parameters.

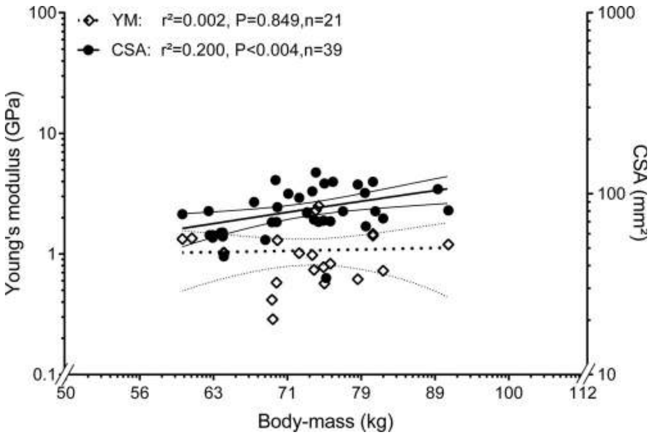

FIGURE 5—Body mass plotted against the Young's modulus and CSA of the PT and AT. Data points were obtained from baseline characteristics of the subjects recruited in short-term intervention studies and the untrained control subjects of comparison studies. The linear regressions and their 95% confidence limits indicate that body-mass correlate with the CSA but not with the Young's modulus.

Time course of material and morphological changes. Similar to the analysis of the dose–response relation, the assessment of the relation between training duration and tendon adaptations did not reveal any clear incremental pattern (Figs. 4A–F). Once more, this inconsistency should be considered carefully in relation with possible methodological differences between studies and with the limited amount of available data outside the 6- to 14-wk range of training duration. Nonetheless, these findings are partially in line with longitudinal observations from one training study (38). In their report, Kubo et al. (38) described that AT stiffness did not change significantly after 8 wk of IR training despite a 19% increase muscle strength whereas stiffness increased by a sizable 50% after 12 wk. Our analysis suggests that tendon stiffness, and often modulus, can increase as early as 6–8 wk into the training program, but it also corroborates the lack of progressive increase in this parameter (Fig. 4A–B and D–E). Taken together, these findings may highlight the current limitations of *in vivo* techniques used to measure changes in tendon properties, lacking the sensitivity required to detect early changes smaller than approximately 20%. Interestingly, no difference in the Young's modulus was observed between trained and control tendons in cross-sectional studies (9,65,67). In contrast, Figure 4C and F indicate that tendon CSA of long-term athletes can exceed that of controls by at least 20%. However, the relatively small (approximately 5%) tendon hypertrophy observed in some training studies suggests that this process is slower than changes in material properties.

Because tendinous stiffness originates from tendon material properties and/or morphology, these results imply that short-term adaptation to increased loading is driven by changes in material properties. The present findings, which are insufficient to yield the precise time-course of tendon material and morphological changes to training, may nonetheless support a unifying theory of tendon adaptive mechanisms when considered in the broader context of data obtained from cross-species comparisons.

Adaptive mechanisms and model. The increase in tendon stiffness found with resistive exercise may be explained by the same twofold mechanisms hypothesized to explain tendon tissue maintenance (29,30,73). On one hand, an increase production of ECM proteins stemming from the mechanotransductive response of fibroblasts may serve to optimize force transmission and/or strengthen tendons (30). On the other hand, fatigue damage occurs at relatively low stress levels (72) and routine remodeling and repair of the collagenous scaffold seem to be inherent features of tendons' design and maintenance. Either way, the integration

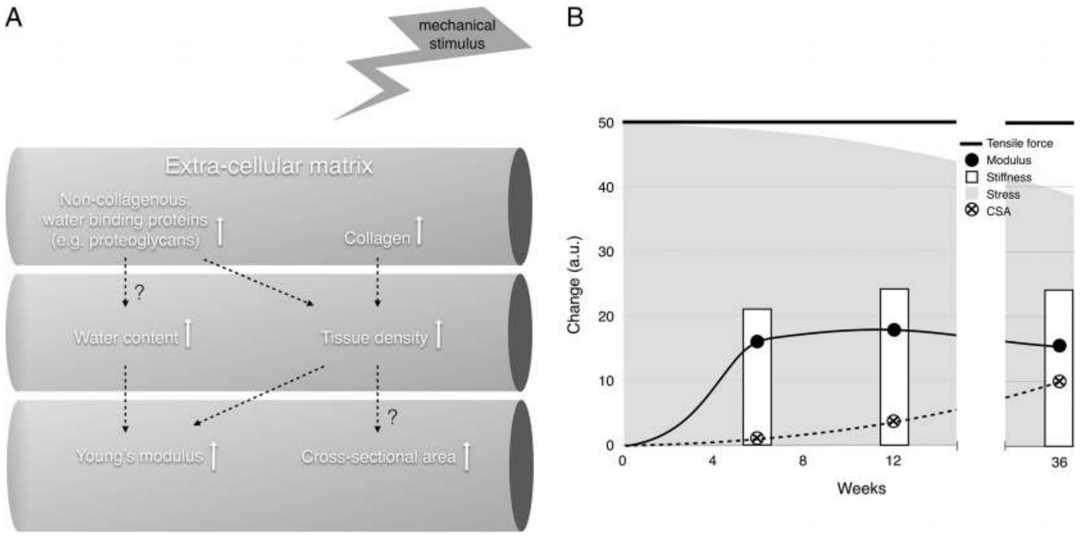

FIGURE 6—Hypothetical model of adaptive mechanisms. A. This panel shows the theoretical connection between training-induced changes in tendon material properties and hypertrophy. *White arrows* denote an increase in molecule production or in a variable. *Dashed arrows* denote a causal link. *Question marks* denote an unproven link. B. This panel illustrates the concept with a unitless graph of the time course of changes that may occur during short- and long-term training at constant loading.

of synthesized collagen into the tendon structure is poorly understood but the present review confirms that this process may promote growth and/or a change in material properties. Because tendon hypertrophy seems limited or insubstantial after short-term resistance training and because an increase in the Young's modulus is almost systematically reported, the latter may constitute the main adaptive process by which the tendon becomes stiffer in the first weeks.

At first glance, this interpretation contrasts with findings from animal studies showing that the mass of quadrupedal mammals scales with the CSA of their limb tendons but not with the Young's modulus (28,61). Indeed, because the daily stress imposed on animal tendon is related to their body mass, tendon CSA—not material properties—can be seen as an adjusting factor to accommodate different levels of stress. In fact, we propose here to extend this theory to explain the training-induced changes observed in human tendons. In agreement with the previously mentioned animal studies, our analysis shows a positive correlation between the body mass of untrained human subjects and the CSA of their lower limb tendons but not with their Young's modulus (Fig. 5).

These findings confirm that tendon hypertrophy is a slow process. However, the rapid metabolic response (see "Introduction" section) taking place in the tendon also indicates that tissue remodeling occurs within the first days after exercise. The production of ECM proteins may be drawn toward internal remodeling of the collagenous scaffold, in turn increasing tissue density and mechanically increasing tendon Young's modulus. In support of this theory, collagen concentration alone (i.e., irrespective of its integration to the ECM architecture) has been shown to affect tendon mechanical properties (75). This phenomenon may take place until a critical density is reached to enable tendon growth. In addition, the increase in production of water-binding proteins such as proteoglycans (15) may be sufficient to increase tendon hydration and, *de facto*, increase stiffness and modulus (20). Hence, we hypothesize that changes in tendon material properties and size are part of the same continuum, driven by daily stresses and ECM protein density. In this context, the changes in material properties seen in the early stage of training may be transient. The density of the ECM may decrease to minimize the energetic cost of maintenance when sufficient growth has occurred (Fig. 6). The fact that all resistance training studies used a progressive increment of load implies that stress levels were increased throughout training, maintaining elevated levels of protein synthesis and tensile modulus.

The theoretical framework supporting this model extends beyond the scope of the present work, yet the same paradigms regulating the design of load-bearing tissue may hold true, with tendon safety factor (i.e., operating stress relative to failure stress) and functional requirements defining an adaptive threshold (6).

Suggestions for future research. The present work highlighted several gaps in the literature regarding the adaptations of human tendons to training. First, any analysis of the relative contribution of material and morphological changes to increased tendon stiffness is limited by the small number of studies reporting all three parameters (PT (10,33,44,55,56,63,66,67) and AT (26,65)). Second, training studies lasting less and more than the typical 12- to14-wk time window are currently lacking, restricting the time-course analysis. Third, most of the research on tendon adaptations is focused on resistance training. Comparatively, only little information is available regarding the effects of exercise implying different loading configurations, such as plyometric training or running. These forms of training arguably involve the capacity of tendons to store and release energy and are essential to a holistic view of tendon adaptations to increased loading. In addition, training studies should also consider the "free" AT exclusively. Research has shown that properties of this portion are different from those of the whole AT (51), and hypertrophy has thus far only been detected in the "free" tendon region (1,65); yet changes in mechanical and material properties in this tendon portion specifically have rarely been reported. Another gap revealed by the present review relates to the changes in tendon capacity to store and release energy. Only a handful of studies have thus far assessed the influence of training upon tendon hysteresis and we currently lack sufficient data for a solid appraisal. Finally, the important variability in reported changes certainly hinders the resolution of any analysis. Previous authors (e.g., 21) have pointed at the methodological heterogeneity of tendon training studies. A larger consensus on methodologies used to test tendon *in vivo* is required to improve the accuracy of future studies.

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